

Phase Transition in an Exactly Solvable Extinction Model

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We introduce a model of biological evolution where species evolve in response to biotic interactions and a fluctuating environmental stress. The species may either become extinct or mutate to acquire a new fitness value when the *effective* stress level is greater than their individual fitness. The model exhibits a phase transition to a completely extinct phase as the environmental stress or the mutation rate is varied. We discuss the generic conditions for which this transition is continuous. The model is exactly solvable and the critical behavior is characterized by an unusual dynamic exponent $z = 1/3$. Apart from predicting large scale evolution, the model can be applied to understand the trends in the available fossil data.

An important question that intrigues both scientists and non-scientists alike, is that of the origin and evolution of life on this planet. Where did all the diverse variety of species on earth come from? Why did some of the species which initially existed, got wiped out while others survived? What are the factors influencing the process of mass extinction? These have emerged as a multi-disciplinary field of research over the last few decades, attracting attention of researchers from various branches of science. The phenomenon of species extinction is an equally important event, and is an inextricable part of the evolution process. In recent times, several models of evolution and extinction have been proposed. Some early evolution models have considered evolutionary dynamics of interacting species on a rugged *fitness landscape* [1, 2]. In these models, under repeated mutation and selection *fit* species tend to *climb up* on the fitness landscape until a local maximum or peak is reached. The landscape may also be coevolving with the evolution of the species. A pioneering work by Bak and Sneppen [3] modeled the extinction of coevolving species on a fitness landscape as a self-organized critical (SOC) process. Here, coevolution of species can trigger *coevolutionary avalanches* of extinction events and the avalanche size is distributed algebraically with an universal exponent τ in the range $1 \leq \tau \leq \frac{3}{2}$ [4]. However, a major drawback of these models is that they completely ignore the role of the environmental stresses e.g., climatic, geological or exogenous stresses [4]. Recently, Newman [5] has proposed a model considering only environmental stresses as the cause of large scale extinction, which can explain the trends in the available fossil records [6].

In this article, we study a model of biological evolution taking into account both external stresses as well as biotic interactions between species as contributory factors for species extinction. Here, less fit species either become extinct or they mutate, due to changes in environmental stress level. Biotic interaction is incorporated as *cooperativity* among the species, which has not been considered in any of the models mentioned above. It

is well known that cooperativity is an important factor for proper functioning of every ecosystem which arises from the interdependence between species, e.g., *via* the food web [7]. Such interactions at the level of individual species are in fact important in modeling evolution and extinction on ecological time scales, as has been argued in Ref. [8].

We show that, a phase transition leading to a complete extinction of the species may occur in this model, as the environmental stress is increased. Generally such a transition occurs discontinuously and only under specific conditions it becomes continuous. For the continuous transition, the critical value of the stress, the critical exponents $(\alpha, \beta, \nu_{||}, \nu_{\perp}, z)$ and the scaling functions can be calculated analytically. The critical behavior of the system is found to be robust against the variation of mutation rate and the fluctuations in stress.

Let us now describe the model in detail. We consider an ecosystem consisting of N different species and let x_i ($i = 1, 2, \dots, N$) denote the fitness of the i^{th} species. The fitness x_i is drawn from a fitness distribution $\mathcal{F}(x)$. The species are subjected to a fluctuating environmental stress \mathcal{S} which is drawn from a distribution $\mathcal{D}(\mathcal{S})$. However, due to the presence of cooperativity, the existing species in the ecosystem experience an *effective* stress $s = \mathcal{S}/\mathcal{C}$, where \mathcal{C} is the measure of cooperativity among the species. Thus, for a given environmental stress \mathcal{S} , the effective stress is smaller when cooperativity among species is large and vice-versa. In general, $\mathcal{C}(N_t)$ depends on the existing number of species N_t at time t . If the number of existing species is very large, they compete for resources e.g., food, habitat etc. and their cooperativity decreases. Thus $\mathcal{C}(N_t)$ is expected to be a decreasing function for large N_t . However, for very small N_t , the species tend to cooperate for survival. In this regime, the resulting cooperativity $\mathcal{C}(N_t)$ is an increasing function.

Extinction of species in our model occurs as follows. At any instant t , species whose fitness x_i is numerically smaller than the effective stress $s_t = \mathcal{S}_t/\mathcal{C}(N_t)$, either become extinct with rate p , or mutate with rate $(1 - p)$ to a new fitness x_i randomly drawn from the distribution $\mathcal{F}(x)$. Note that the renewed fitness value may be either same, greater, or smaller as compared to the current

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value of the species fitness, and correspond to a neutral, favorable or an harmful mutation respectively.

Since in our model the extinct species are not repopulated by new ones, the number of existing species N_t , and therefore, the density $\rho_t = N_t/N$, can only decrease with time. The new effective stress is then $s_{t+1} = S_{t+1}/\mathcal{C}(N_{t+1})$, where, S_{t+1} is a new environmental stress value drawn from $\mathcal{D}(\mathcal{S})$. The dynamics stops when either all the surviving species are fit, or none of them survive under the applied stress. Therefore, depending on the environmental stress there is a possibility of complete extinction of the species. This transition, from a phase with finite population to complete extinction, may occur continuously or abruptly as $\langle S \rangle = \int S \mathcal{D}(\mathcal{S}) dS$ is increased. We will characterize this transition in detail considering $\sigma = \langle S \rangle/N$ and p as control parameters, and provide a phase diagram in the $p - \sigma$ plane.

First, let us assume that, (i) the resources are infinite and therefore, the cooperativity $\mathcal{C}(N_t)$ increases monotonically, say linearly, with N_t , i.e., $\mathcal{C}(N_t) = N_t$ and (ii) the environmental stress \mathcal{S} do not fluctuate in time, i.e., $\mathcal{D}(\mathcal{S}) = \delta(\mathcal{S} - S_a)$. The more general cases, like different functional forms of $\mathcal{C}(N_t)$ and effects due to fluctuation in the stress will be discussed at the end.

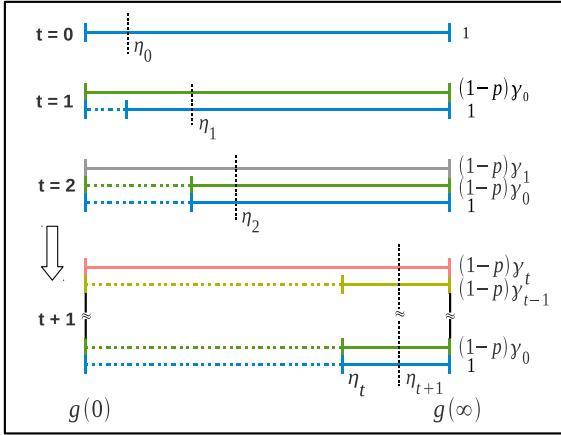


FIG. 1. (Color online) Schematic description of the removal and renewal events. The x -axis represents the cumulative distribution, which extends from $g(0) = 0$ to $g(\infty) = 1$. At a given time t , the species which are surviving (extinct) are denoted by solid (dotted) horizontal lines and a marker $\eta_t = g(\sigma/\rho_t)$ is used to indicate the point below which the species are considered *unfit*. Of these surviving *unfit* species (their density is γ_t), $1 - p$ fraction will mutate to have new fitness values extending over the whole range, increasing the density of surviving species at $t + 1$ by $(1 - p)\gamma_t$. Effectively, at $t + 1$ all the solid lines up to η_t are removed and one additional solid line with weight $(1 - p)\gamma_t$ is drawn.

Starting from an initial density $\rho_0 = 1$, the density of existing species evolves as,

$$\rho_{t+1} = \rho_t - p\gamma_t = \rho_0 - p \sum_{t'=0}^t \gamma_{t'} \quad (1)$$

where, γ_t is the density of the *unfit* species at time t , i.e. $N\gamma_t$ is the number of existing species with fitness value smaller than $S_a/N_t = \sigma/\rho_t$. Clearly, p fraction of $N\gamma_t$ species becomes extinct, and $1 - p$ fraction undergo mutation, acquiring new fitness value spanning the entire range of distribution function $\mathcal{F}(x)$.

Effectively, the above dynamics amounts to the removal of all the $N\gamma_t$ unfit species from the system at time t , and introducing $N(1 - p)\gamma_t$ species with renewed fitness value. The time sequence of such *removal* and *renewal* events are schematically shown in Fig. 1. The solid horizontal lines extending from $g(0) = 0$ to $g(\infty) = 1$ represent the density of species which underwent mutation at the previous time instant and is equal to $(1 - p)\gamma_t$; $g(x) = \int_0^x \mathcal{F}(x') dx'$ is the cumulative distribution function. The dashed lines correspond to the species which have been removed from the system. Utilizing this, it is easy to calculate the density of unfit species γ_{t+1} and is equal to the weighted sum of the length of solid lines upto η_t , with the weight factors $(1 - p)\gamma_t$, where,

$$\eta_t = \int_0^{\sigma/\rho_t} \mathcal{F}(x) dx = g(\sigma/\rho_t)$$

as shown in Fig. (1). Thus,

$$\gamma_{t+1} = (\eta_{t+1} - \eta_t) \left[1 + (1 - p) \sum_{t'=0}^{t-1} \gamma_{t'} \right] + (1 - p)\gamma_t \eta_{t+1} \quad (2)$$

Eqs. (1) and (2) describe the dynamical rules of our model and can be recast into a simple form using

$$\begin{aligned} \pi_{t+1} &= \sum_{t'=0}^t \gamma_{t'}; \\ \pi_{t+1} &= \eta_t [1 + (1 - p)\pi_t] \\ \rho_{t+1} &= \rho_0 - p\pi_{t+1} = 1 - p\eta_t [1 + (1 - p)\pi_t] \end{aligned} \quad (3)$$

When mutation is absent ($p = 1$), this set of equations Eq. (3) reduces to $\rho_{t+1} = 1 - \eta_t$. This special case of our model, with $\mathcal{C}(N_t) = N_t$ and $\mathcal{D}(\mathcal{S}) = \delta(\mathcal{S} - S_a)$ has been studied earlier [9] as the *democratic Fiber Bundle Model* (dFBM) in the context of failure processes. In the dFBM model, a heavy load weighing S_a hangs from a rigid anchor by a bundle of N elastic fibers, each having a certain breaking strength x_i . Initially, all the fibers are intact and share the applied load equally, each experiencing an effective load S_a/N . At each time step, weaker fibers (fibers with strength less than the effective load) fail, and the load is re-shared equally among the remaining intact fibers. Thus the effective load per fiber increases creating an avalanche of failure events. If the initial load S_a is low, this process reaches a stationary state with some intact fiber which eventually support the load, whereas a complete failure occurs for high S_a . Thus, at some critical value of S_a the dFBM model exhibits a breakdown transition which may be abrupt or continuous[10].

Coming back to the general case $p \neq 1$, let us first compute the fixed points of Eq. (3), where $\pi_{t+1} = \pi_t =$

π^* and $\rho_{t+1} = \rho_t = \rho^*$. Thus, we have $\pi^* = g(\sigma/\rho^*)[1 + (1-p)\pi^*]$ and

$$\rho^* = 1 - p\pi^* = \frac{1 - g(\sigma/\rho^*)}{1 - (1-p)g(\sigma/\rho^*)}. \quad (4)$$

This equation may have multiple solutions for ρ^* ; the largest among them $\rho_s = \text{Max}(\rho^*)$ is stable since the right hand side of Eq. (4) is a non-decreasing function of ρ^* bounded in the range $(0, 1)$. Therefore, starting from the initial density $\rho_0 = 1$, the density decreases and eventually approaches a stationary value ρ_s .

The steady state density ρ_s is the rightmost intersection point of the curves

$$y = \sigma x \quad \text{and} \quad y = G(x) = \frac{1 - g(1/x)}{1 - (1-p)g(1/x)}, \quad (5)$$

where x replaces ρ^*/σ in Eq. (4) and $G(x)$ is a non-decreasing function with $G(0) = 0$ and $G(\infty) = 1$. Clearly, these two curves intersect at $x = 0$ for all values of σ . If the curves intersect at other points ($x > 0$), the rightmost one, (say) x_s correspond to the steady state density $\rho_s = \sigma x_s$. This is described schematically in Fig. 2a. Existence of a solution $\rho_s > 0$ indicates that the system is in a non-extinct phase while complete extinction occurs when the only solution is $\rho_s = 0$.

The transition point between the two phases and the order of the transition can be determined from the behavior of $G(x)$. Consider that $G(x)$ is bounded from above by the a line $y = \tilde{\sigma}x$ such that $G(x) \leq \tilde{\sigma}x \quad \forall x$. Let this line be a tangent of $G(x)$ at some $x = \tilde{x}$. If the line is a tangent at multiple points (see Fig. 2b), the rightmost one will be \tilde{x} . Clearly the system is in (non-)extinct phase for any σ (smaller) greater than $\tilde{\sigma}$. So, at the transition point $\sigma_c = \tilde{\sigma}$ the order parameter is $\rho_s = \tilde{\sigma}\tilde{x}$. The transition will be discontinuous when \tilde{x} is nonzero, since in this case the order parameter has a nonzero value at the critical point (see Fig. 2b). A continuous transition occurs if $\tilde{x} = 0$, and the critical point is, therefore, $\sigma_c = \tilde{\sigma} = G'(0)$. This implies that the transition is continuous only if the tangent line of $G(x)$ at $x = 0$ bounds the curve from above, i.e., when $G(x)/x \leq G'(0) \quad \forall x$ (see Fig. 2a).

It may be mentioned here that the extinction transition will be discontinuous if $\mathcal{F}(x)$ has a cut-off (say) at x_m , such that $\mathcal{F}(x > x_m) = 0$. This implies that $g(x > x_m) = 1$ and therefore, $G(x < 1/x_m) = 0$. A typical form of such a function, with $x_m = 1$, is shown in Fig. 2b(inset). In this case, the transition will occur discontinuously as $\tilde{x} \neq 0$.

In the following, we discuss the continuous phase transition in detail. Since the critical point $\sigma_c = G'(0)$, is related to $g(x)$ and its derivative as $x \rightarrow \infty$, we expand $g(x)$ as,

$$g(x) = 1 - a(1/x)^\lambda + \dots \quad (6)$$

where a is a positive constant. Thus for $\lambda < 1$, the critical point $\sigma_c = G'(0) = \infty$ and hence complete extinction can never happen. Again, for $\lambda > 1$ the transition is discontinuous as in this case $G'(0) = 0$. Thus, the only

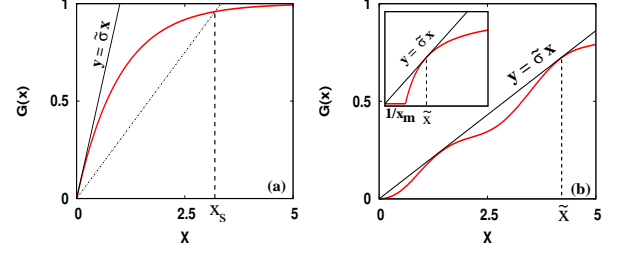


FIG. 2. (Color online) (a) A typical $G(x)$, bounded from above by $y = \tilde{\sigma}x$ where $\tilde{\sigma} = G'(0)$, results in a continuous extinction transition with $\rho_s = \sigma x_s$. (b) For generic $G(x)$ the transition is discontinuous; (inset) $G(x)$ for a bounded fitness distribution (see text).

non trivial extinction phase transition occurs for $\lambda = 1$ where the critical point $\sigma_c = a/p$ is nonzero and finite. Note that the higher order terms in Eq. (6) do not play any role in determining the critical point.

Let us now characterize the phase transition in terms of the critical exponents and the scaling functions. From Eq. (4), it is evident that for small $\varepsilon = \sigma_c - \sigma$, the order parameter $\rho_s = (\varepsilon/\sigma_c)^\beta$, with $\beta = 1$. The scaling functions can be derived from the dynamics of the model near the critical point, which can be approximated, following Eq. (4), by

$$\sigma \rho_{t+1} = \frac{1 - g(1/\rho_t)}{1 - (1-p)g(1/\rho_t)}. \quad (7)$$

Taking the continuum limit and retaining terms upto second order in ρ , we have

$$(a/p - \varepsilon) \frac{d\rho}{dt} = \varepsilon \rho - \frac{a^2(1-p)}{p^2} \rho^2, \quad (8)$$

where $\sigma_c = a/p$. Close to the critical point ($\varepsilon \rightarrow 0$), by rescaling the variable as $\varrho = \varepsilon^{-1}\rho$ and $\tau = \varepsilon t$, Eq. (8) can be written in a scaling form as $\frac{a}{p} \frac{d\varrho}{d\tau} = \varrho - \frac{a^2(1-p)}{p^2} \varrho^2$. The formal solution of this rescaled differential equation can be written in one of the following forms;

$$\rho(\varepsilon, t) = \begin{cases} t^{-\alpha} f_\alpha(\varepsilon^{\nu_\alpha} t) \\ \varepsilon^\beta f_\beta(\varepsilon^{\nu_\beta} t), \end{cases} \quad (9)$$

where, the exponents $\alpha = 1 = \nu_\alpha$. From the scaling relation $\beta = \alpha \nu_\alpha$, we again get $\beta = 1$. The functions $f_\alpha(x)$ and $f_\beta(x)$ can be obtained by solving Eq. (8) with boundary condition $\rho(\varepsilon, 0) = 1$ which gives,

$$f_\alpha(x) = x f_\beta(x) = \frac{p^2 x}{a^2(1-p) + \exp(-px/a)} \quad (10)$$

A finite size scaling relation can also be derived for this model. For a system of size N , the mean number of existing species $\langle N_t \rangle$ will have a finite nonzero value even at the critical point σ_c (see Fig. 3), originating from the large critical fluctuations in N_t . Fluctuations of N_t result from the inherent stochasticity of the fitness values and it is expected that its width will be proportional to $\sqrt{\langle N_t \rangle}$. These fluctuations can be incorporated in the model by modifying the density ρ_t as,

$$\rho_t \rightarrow \rho_t + k\sqrt{\rho_t/N} \quad (11)$$

where, $\rho_t = \langle N_t \rangle / N$, is the mean density and k is a constant of proportionality. Now using Eq. (11) in the Eq. (7) and keeping the leading terms in N and ρ , in the continuum limit we have, $\frac{d\rho}{dt} = k[\sqrt{\rho/N} - K\rho^2]$, which on a rescaling of variables $\varrho = N^{1/3}\rho$ and $\mathfrak{t} = tN^{-1/3}$ yields,

$$\frac{d\varrho}{d\mathfrak{t}} = k[\sqrt{\varrho} - K\varrho^2], \quad (12)$$

where $K = a(1-p)/pk$. The solution $\varrho(\mathfrak{t})$ can be rewritten[11] in the scaling form

$$\rho(N, t) = N^{-\beta/\nu_\perp} f_N(tN^{-z}) \quad (13)$$

where $z = \frac{1}{3} = \beta/\nu_\perp$ (since $\beta = 1$, we have $\nu_\perp = 3$). Note that the dynamical exponent z satisfy the scaling relation $z = \nu_\parallel/\nu_\perp$. The unusually low dynamical exponent signifies the *accelerated* extinction occurring in this model.

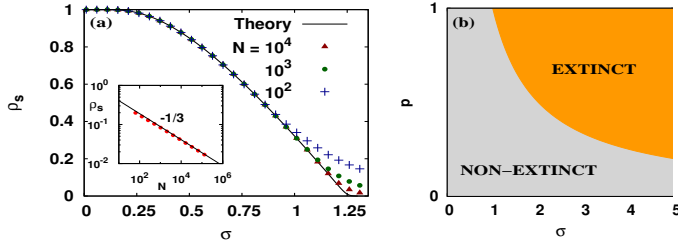


FIG. 3. (Color online) (a) ρ_s as a function of σ for fitness distribution $\mathcal{F}(x) = \exp(-1/x)/x^2$ and $p = 0.8$. Simulation results for different N (symbols) are compared with solution of Eq. (4) (solid line). (inset) log-log plot of ρ_s vs. N at $\sigma_c = 1/p$ is linear with slope $-\beta/\nu_\perp = -1/3$. (b) Phase diagram of the model; complete extinction occurs for $\sigma > \sigma_c = 1/p$.

Until now, we have considered the system with infinite resources which however is unrealistic. For finite resources, the cooperativity function decreases with increase in the number of species N_t , and a generic form can be chosen to be $\mathcal{C}(N_t) = N_t^\theta \exp(-N_t/N_m)$, where the scale N_m is proportional to the total number of species N . In this case, Eq. (1) with $p = 1$ can be written as $\rho_{t+1} = 1 - g\left(\frac{\sigma N^{1-\theta}}{\rho_t^\theta \exp(-\rho_t/\rho_m)}\right)$, where $\rho_m = N_m/N$.

Clearly, in the thermodynamic limit, this dynamics will reach a stationary density $0 < \rho_s < 1$ only for $\theta = 1$. The critical behavior in this case is identical to that of the system with infinite resources.

To demonstrate the continuous extinction transition we choose a specific fitness distribution $\mathcal{F}(x) = x^{-2}e^{-1/x}$ and a linear cooperativity function. The steady state density for $p = 1$ can be calculated exactly using Eq. (4) as $\rho_s = 1 + \sigma W(-\sigma^{-1} \exp(-\sigma^{-1}))$ where $W(x)$ is the Lambert W function. For $p \neq 1$, the solution of Eq. (4) is found to be in excellent agreement with ρ_s obtained from numerical simulations (Fig. 3(a)). The inset shows that $\rho_s \sim N^{-\beta/\nu_\perp}$ with $\beta/\nu_\perp = 1/3$. The line of criticality $\sigma = 1/p$ separates the extinct phase from non-extinct one (Fig. 3(b)). This critical behavior is robust against fluctuations which has been checked numerically by adding gaussian noise to the environmental stress.

In conclusion, we have introduced an exactly solvable evolution model which incorporates some of the important features of biological evolution, namely, extinction of less fit species under environmental stress, cooperativity among the species and mutation. Under fairly general conditions, the model undergoes a discontinuous phase transition into a fully extinct state, whereas for certain specific choice of fitness distribution and cooperativity function the transition occurs continuously. The critical point, the critical exponents ($\alpha, \beta, \nu_\parallel, \nu_\perp, z$) and the scaling functions of the continuous transition are calculated analytically. In particular, the dynamical exponent $z = \frac{1}{3}$ is quite unexpected and implies an *accelerated* species extinction. Apart from predicting large scale evolution *via* a critical dynamics[13] and existence of a completely extinct state, the model can also be applied to understand the trends in the available fossil data, as has been attempted by other models of evolution[4]. Close to criticality, the distribution of extinction events in this model follow a power-law with exponent $\tau = \frac{3}{2}$ (obtained from simulation of the model). Since here the growth exponent $\eta = 0$ (no repopulation), one may argue[12] that $\tau = \frac{1+\eta+2\alpha}{1+\eta+\alpha} = \frac{3}{2}$. In fact, this value is consistent with the distribution of extinct families of marine animal species, where τ varies in the range 1.35 to 1.95[13]. Our model can be extended further to include other complex features e.g., repopulation of extinct species, local inter-species interactions in different dimensions, species dependent external stress, speciation.

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- [1] S. Wright, *Proc. Nat. Acad. Sci.* **58**, 165 (1967).
- [2] S. A. Kauffman and S. Levin, *J. Theor. Biol.* **128**, 1145 (1987).
- [3] P. Bak and K. Sneppen, *Phys. Rev. Lett.* **71**, 4083 (1993).
- [4] M. E. J. Newman and R. G. Palmer, [adap-org/9908002](https://arxiv.org/abs/adap-org/9908002).
- [5] M. E. J. Newman, *J. Theor. Biol.* **189**, 235 (1997).

- [6] J. J. Sepkoski, *Milwaukee Public Museum Contributions in Biology and Geology* **83** (1993).
- [7] B. Drossel and A. J. McKane, *Handbook of Graphs and Networks* (eds. S. Bornholdt and H. G. Schuster), pp. 218-247. Wiley-VCH, Berlin.
- [8] D. Chowdhury and D. Stauffer, *Phys. Rev. E* **68**, 041901

- (2003).
- [9] S. Pradhan, A. Hansen, B. K. Chakrabarti, *Rev. Mod. Phys.* **82**, 499 (2010).
- [10] J. V. Andersen, D. Sornette, and K. Leung, *Phys. Rev. Lett.* **78**, 2140 (1997).
- [11] Solution of Eq. (12) is $\mathfrak{t} = \frac{1}{3k\sqrt[3]{K}}G(\sqrt[3]{K}\varrho)$, where $G(x) = 2\sqrt{3}\tan^{-1}(\frac{1+2x}{\sqrt{3}}) + \log \frac{1+x+x^2}{(1-x)^2}$.
- [12] M. A. Munoz, R. Dickman, A. Vespignani and S. Zapperi, *Phys. Rev. E* **59**, 6175 (1999).
- [13] R. V. Sole and J. Bascompte, *Proc. R. Soc. London B* **263**, 161 (1996).